

SHORT COMMUNICATION

Notes on a *Mesodinium rubrum* red tide in San Francisco Bay (California, USA)

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Abstract. Discrete red patches of water were observed in South San Francisco Bay (USA) on 30 April 1993, and examination of live samples showed that this red tide was caused by surface accumulations of the pigmented ciliate *Mesodinium rubrum*. Vertical profiles showed strong salinity and temperature stratification in the upper 5 m, peak chlorophyll fluorescence in the upper meter, and differences in the small-scale density structure and fluorescence distribution among red patches. Events preceding this *Mesodinium* red tide included: (i) heavy precipitation and run-off, allowing for strong salinity stratification; (ii) a spring diatom bloom where the chlorophyll *a* concentration reached 50 mg m⁻³; (iii) depletions of dissolved inorganic N and Si in the photic zone; and (iv) several days of rapid warming and stabilization of the upper surface layer. These conditions may be general prerequisites for *M. rubrum* blooms in temperate estuaries.

During a cruise to map the hydrography of South San Francisco Bay (California, USA) on 30 April 1993, we observed a red tide in the lower estuary that was manifested as (i) narrow streaks of pigmented water aligned with axial fronts (foam lines) that formed in the channel during the ebbing tide and (ii) discrete irregular red patches of variable dimension (~10–50 m), distributed across the deep channel and the subtidal shallows of the lower Bay (Figure 1). Microscopic examination of live samples from these patches revealed a microplankton community dominated by the phototrophic ciliate *Mesodinium rubrum*. *Mesodinium rubrum* is a common species in South San Francisco Bay during spring, typically present at low abundances, but occasionally reaching very high population densities (>10³ cells ml⁻¹, Wong and Cloern, 1982) within patchy red tides that develop and become visible at the water surface.

Mesodinium rubrum is a cosmopolitan species that episodically reaches bloom densities in temperate coastal waters, upwelling zones and estuaries (Lindholm, 1985; Crawford, 1989). Barber and Smith (1981) proposed a mechanism for bloom formation in upwelling zones, where the combined motions of two-layer flow and diel vertical migrations of *M. rubrum* can act to maintain cells within dense aggregations. Mechanisms for bloom formation of this species within estuaries may be more complex. For example, Crawford and Purdie (1992) observed vertical migrations of *M. rubrum* over a tidal cycle in Southampton Water, and they interpreted these migrations as active avoidance of turbulence generated in the surface layer during ebb flows, a behavior that would act to retain the population within the estuary. Most recorded *Mesodinium* red tides

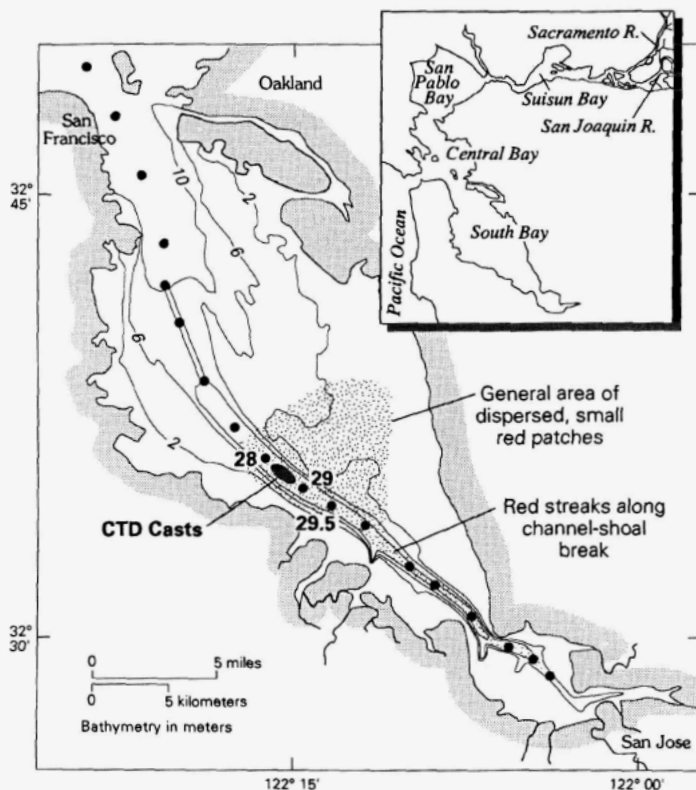


Fig. 1. Map of South San Francisco Bay showing the locations of fixed sampling stations, the approximate position of the red tide patches sampled by CTD-fluorometry and the general region of pigmented water (shaded area).

have been observed with discrete sampling, so fine-scale vertical distributions of this motile organism are not well characterized (however, see Lindholm and Mork, 1990). We had an opportunity to measure the vertical distributions of chlorophyll fluorescence (and, presumably, *M. rubrum* biomass) within several red patches during the April 30 cruise. Phytoplankton biomass and hydrography were also measured during the preceding 2 months, and this record of observation provides a basis for proposing a general set of conditions that might promote the development of *M. rubrum* red tides in temperate estuaries.

During March and April of 1993, weekly cruises were conducted to map vertical distributions of salinity, temperature, and concentrations of chlorophyll *a* (chl_a), dissolved oxygen (DO) and suspended particulate matter (SPM). Vertical profiles were obtained at fixed sampling locations spaced approximately every 3 km along the deep channel (Figure 1). Conductivity, temperature and pressure were measured with a Sea-Bird Electronics SBE9/11 CTD configured to sample at 24 Hz and lowered through the water column at a rate of ~ 0.5 – 1.0 m s^{-1} . Hence, measurements were vertically spaced about every 2–4 cm.

Parallel measurements were made of chlorophyll fluorescence using a SeaTech *in vivo* fluorometer, DO with a YSI 5739 oxygen electrode, SPM with a Sea-Bird OBS-3 optical backscatter sensor and photon flux density with a LiCor 192S quantum sensor. The fluorometer was calibrated each cruise with discrete measures of *chl a* determined spectrophotometrically from samples collected onto GF/AE filters (Lorenzen, 1967). Live samples were periodically examined microscopically (400 \times) to document the composition of the most abundant phytoplankton taxa. On some cruises, nutrient concentrations, including dissolved silica (DSi) and dissolved inorganic nitrogen (DIN = nitrate + nitrite + ammonium), were measured in near-surface samples collected by pump at every station. Nutrient concentrations were determined on samples passed through 0.4 μ m Nuclepore filters, using a continuous-flow autoanalyzer and procedures described by Hager (1993).

During the course of sampling on April 30, we lowered the CTD-fluorometer through three discrete patches of red water located between stations 29 and 28 (Figure 1). The time of sampling (11:40 Pacific Daylight Time) coincided closely with the time of predicted maximum ebb-tide current; opposing winds from the northwest accelerated during the morning and averaged 7 m s⁻¹ at the time of sampling. The discrete patches were small (<50 m) and the sequential CTD casts were made within a period of 5 min. Vertical distributions of salinity, temperature and *in vivo* fluorescence from the three casts are shown in Figure 2. Although the three casts were made closely in time and space, each showed unique vertical patterns, presumably because of the ephemeral nature of these distributions during periods of wind-driven and tidal advection and mixing. For example, the first cast at 11:36 h showed a thin lens of low-salinity water in the upper 20 cm of the water column, and relatively uniform salinity below 1 m (Figure 2). This cast revealed a fluorescence maximum in the upper meter and a sharp fluorescence gradient between 1 and 2 m. Cast no. 2 at 11:38 h showed different vertical distributions with a sharp halocline at 5 m, a more gradual salinity gradient in the upper 5 m and small-scale salinity fluctuation in the upper 1–2 m, indicating an unstable density distribution, probably resulting from wind-driven overturning. The temperature distribution mirrored salinity, and the fluorescence distribution was similar with two distinct peaks in the upper 1.5 m. Cast no. 3 at 11:41 h also showed large salinity fluctuation in the upper 5 m, with a sharp halocline in the upper meter and evidence of overturning at the surface. In this case, a fluorescence peak was observed at ~0.5 m depth, within the sharp upper halocline and upper thermocline. Below this peak, fluorescence declined gradually down to ~5 m.

Although the three vertical casts showed different small-scale variability, each had the following general features. First, each revealed strong salinity, temperature (and, therefore, density) stratification with the primary pycnocline above 5 m depth. Although most of the density gradient resulted from the salinity distribution, temperature gradients in the upper 5 m were also large. Second, the fluorescence profiles all showed minimum fluorescence (corresponding to a *chl a* concentration of ~2 mg m⁻³) at depth, and peak fluorescence (corresponding to a *chl a* concentration of ~15–20 mg m⁻³) in the upper 1–1.5 m

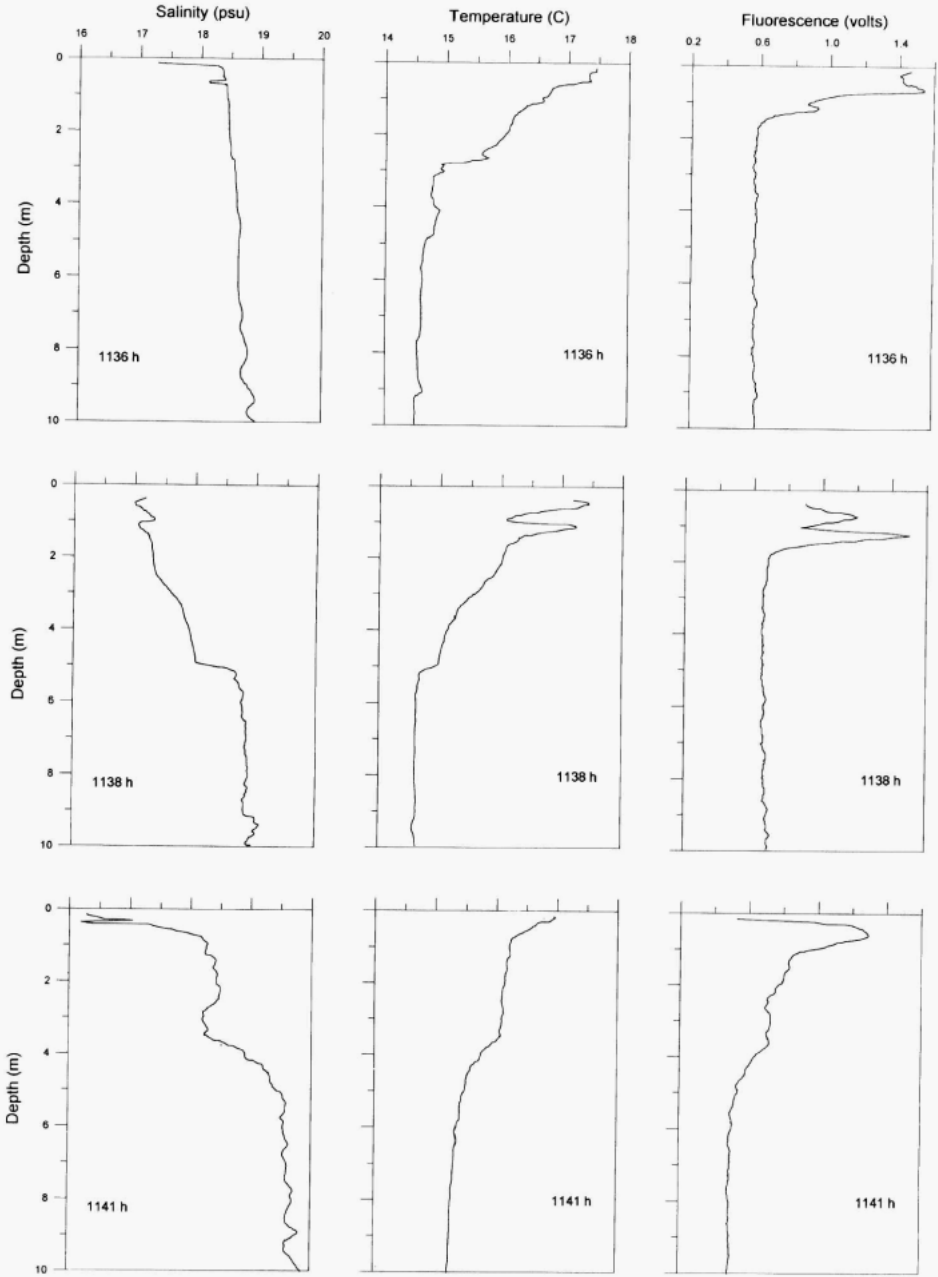


Fig. 2. Vertical distributions of salinity, temperature and *in vivo* fluorescence in the upper 10 m, from sequential CTD-fluorometer casts in three red-tide patches of South San Francisco Bay (see Figure 1).

of the water column. Third, there was no obvious correlation between the vertical positions of the fluorescence peaks and the density distributions (the fluorescence peaks were found above the depth of 1% surface irradiance located at 3.2–3.6 m in these casts). These features suggest that vertical distributions of chlorophyll fluorescence were not controlled by mixing processes. *Mesodinium rubrum* is capable of rapid swimming speeds ($>5 \text{ m h}^{-1}$; Barber and Smith, 1981), so the fluorescence peaks in the upper meter may have resulted from this species' strong phototactic behavior. However, these snapshot profiles may represent only one phase of a vertical migration cycle cued to the tides, such as that observed by Crawford and Purdie (1992).

Events preceding the April 30 red tides in South San Francisco Bay may give clues about the general conditions necessary for *M. rubrum* bloom formation within estuaries. Figure 3 shows weekly changes in surface salinity, surface

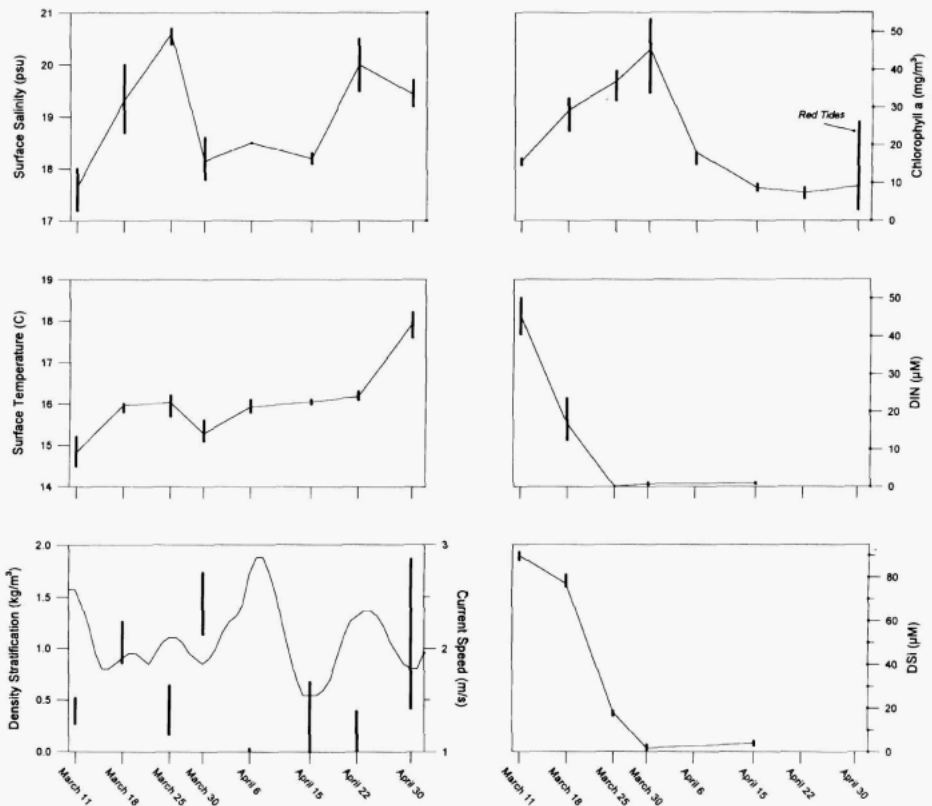


Fig. 3. Weekly changes in lower South San Francisco Bay from 11 March to 30 April 1993. Vertical bars show the range of measurements made at stations 28, 29, 29.5 and 30, from samples in the upper 1–1.5 m. Fine lines connect means of these measurements for each sampling date. Individual panels show changes in surface salinity, temperature, density stratification (σ_t difference between 10 m and 1 m), chl*a*, DIN and DSI concentrations. The lower left panel also shows the daily maximum predicted tidal current speed (continuous line) at the entrance to San Francisco Bay (from NOAA tide tables).

temperature and density stratification (σ_t difference between 10 m and 1 m) in the general location of the estuary where the most intense red tide patches were observed. Notable features of the physical environment included: (i) unusually low surface salinity resulting from above-normal precipitation and run-off during spring 1993; (ii) rapid warming ($\sim 2^\circ\text{C}$) of the surface layer during the last week of April, a period of warm sunny weather; (iii) week-to-week fluctuations in density stratification, with persistent stratification during the 3-week period of weak tides in March, destratification during the spring tide beginning around April 6 and re-establishment of stratification during neap tides of April, especially on April 30. This correlation between stratification and tidal currents has been observed previously in South San Francisco Bay (Cloern, 1984) and other tidal estuaries.

Phytoplankton biomass was highly variable during this 2-month period. Chlorophyll *a* concentrations increased steadily throughout March (Figure 3) when the lower estuary was persistently stratified. This March bloom was dominated by coastal diatoms including *Thalassiosira* spp., *Coscinodiscus* spp. and *Ditylum brightwellii*. Phytoplankton biomass declined after the spring-tide destratification in early April, and this pattern of bloom evolution is consistent with past observations of biomass increase during periods of sustained density stratification and reduced vertical mixing (e.g. Cloern, 1991). The *M. rubrum* red tide reported here occurred under conditions of strong density stratification during the last neap tide of April (Figure 3).

Nutrient concentrations were also highly variable and reflected rapid phytoplankton uptake during the March diatom bloom. Surface concentrations of DIN declined from 40–50 μM on March 11 to $<0.1 \mu\text{M}$ on March 25; DIN concentrations in the surface layer remained low ($<1 \mu\text{M}$) on April 15 (Figure 3). Dissolved silica concentrations varied similarly, decreasing from 90 μM on March 11 to a range of 0.9–3.1 μM on March 30 (Figure 3). Nutrient concentrations were not measured at depth on these cruises, but past measurements (Hager, 1993) have shown the most severe depletions of DIN in the surface layer, and especially when the water column is density stratified. These vertical gradients reflect the large benthic source of regenerated DIN (Caffrey, 1992) and the large DIN sink from phytoplankton uptake in the shallow euphotic zone.

Our observations in South San Francisco Bay are consistent with the hypothesis that two conditions are required for *M. rubrum* bloom formation in estuaries. The first is a physical environment of weak turbulent mixing that allows for the rapid production of biomass in the euphotic zone, and the maintenance of that biomass in the surface layer by phototaxis [or the behavioral response to small-scale turbulence proposed by Crawford and Purdie (1992)]. Turbulent mixing is damped in estuaries by salinity stratification following inputs of fresh water, and by thermal stratification during periods of rapid warming of the surface layer. Turbulence generation increases with tidal stresses at the bed and wind stress at the surface. So, an optimal physical environment for *M. rubrum* bloom development in estuaries would result from a scenario of large seasonal inputs of freshwater (buoyancy), followed by episodes of simultaneous

neap tides and warm, stable weather (see Packard *et al.*, 1978). This physical environment can apparently occur in South San Francisco Bay only during the spring season of wet years because *M. rubrum* red tides were not observed during the sustained drought from 1987 to 1992. However, large, widely distributed red tides did develop during the springs of 1982 and 1983, periods of exceptionally high precipitation and river run-off; these past red-tide events all coincided with neap tides and hot, stable weather.

Physical environments of weak turbulent mixing may not be sufficient to allow for the development of *M. rubrum* blooms because such physical regimes can promote biomass production by other species as well. The April 1993 red tides in South San Francisco Bay occurred after the surface concentrations of DIN and DSi had been greatly reduced by antecedent diatom blooms, similar to observations in other estuaries (Kifle and Purdie, 1993). *Mesodinium rubrum* red tides appear to develop in a chemical environment where competing species, such as diatoms, may be resource limited, either because of Si depletion or their inability to migrate vertically and exploit the pools of DIN below the pycnocline and euphotic zone (Lindholm and Mork, 1990). From this perspective, *M. rubrum* might be considered an ecological analog to dinoflagellates. However, the exceptional swimming capability and complex behavior of this species appear to be particular adaptations that allow for its rapid population growth, and the formation of visible aggregations during episodes of strong stratification and nutrient depletion of near-surface coastal waters.

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References

- Barber, R.T. and Smith, W.O., Jr (1981) The role of circulation, sinking, and vertical migration in physical sorting of phytoplankton in the upwelling center at 15°S. In Richards, F.A. (ed.), *Coastal Upwelling, Coastal and Estuarine Sciences I*. American Geophysical Union, Washington DC, pp. 366–371.
- Caffrey, J.M. (1992) Ammonium regeneration rates and pool sizes in San Francisco Bay sediments. *Program Abstracts, 1992 ASLO Meeting*, Santa Fe, NM.
- Cloern, J.E. (1984) Temporal dynamics and ecological significance of salinity stratification in an estuary. *Oceanol. Acta*, 7, 137–141.
- Cloern, J.E. (1991) Tidal stirring and phytoplankton bloom dynamics in an estuary. *J. Mar. Res.*, 49, 203–221.
- Crawford, D.W. (1989) *Mesodinium rubrum*: the phytoplankter that wasn't. *Mar. Ecol. Prog. Ser.*, 58, 161–174.
- Crawford, D.W. and Purdie, D.A. (1992) Evidence for avoidance of flushing from an estuary by a planktonic, phototrophic ciliate. *Mar. Ecol. Prog. Ser.*, 79, 259–265.
- Hager, S.W. (1993) Dissolved nutrient and suspended particulate matter data for the San Francisco Bay estuary, California, October 1988 through September 1991. *US Geological Survey, Open-File Report 93-57*, 52 pp.

- Kifle,D. and Purdie,D.A. (1993) The seasonal abundance of the phototrophic ciliate *Mesodinium rubrum* in Southampton Water, England. *J. Plankton Res.*, **15**, 823–833.
- Lindholm,T. (1985) *Mesodinium rubrum*—a unique photosynthetic ciliate. *Adv. Aquat. Microbiol.*, **3**, 1–48.
- Lindholm,T. and Mork,A.-C. (1990) Depth maxima of *Mesodinium rubrum* (Lohmann) Hamburger & Buddenbrock—Examples from a stratified Baltic Sea Inlet. *Sarsia*, **75**, 53–64.
- Lorenzen,C.J. (1967) Determination of chlorophyll and phaeopigments: spectrophotometric equations. *Limnol. Oceanogr.*, **12**, 343–346.
- Packard,T.T., Blasco,D. and Barber,R.T. (1978) *Mesodinium rubrum* in the Baja California upwelling system. In Boje,R. and Tomczak,M. (eds), *Upwelling Ecosystems*. Springer-Verlag, pp. 73–89.
- Wong,R.L.J. and Cloern,J.E. (1982) Plankton studies in San Francisco Bay. IV. Phytoplankton abundance and species composition, January 1980–February 1981. *US Geological Survey Open-File Report 82-443*, 152 pp.

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